Elephant cognition in primate perspective

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On many of the staple measures of comparative psychology, elephants show no obvious differences from other mammals, such as primates: discrimination learning, memory, spontaneous tool use, etc. However, a range of more naturalistic measures have recently suggested that elephant cognition may be rather different. Wild elephants sub-categorize humans into groups, independently making this classification on the basis of scent or colour. In number discrimination, elephants show no effects of absolute magnitude or relative size disparity in making number judgements. In the social realm, elephants show empathy into the problems faced by others, and give hints of special abilities in cooperation, vocal imitation and perhaps teaching. Field data suggest that the elephant's vaunted reputation for memory may have a factual basis, in two ways. Elephants' ability to remember large-scale space over long periods suggests good cognitive mapping skills. Elephants' skill in keeping track of the current locations of many family members implies that working memory may be unusually developed, consistent with the laboratory finding that their quantity judgements do not show the usual magnitude effects.

Keywords: *Loxodonta*, *Elephas*, cognitive maps, social knowledge, social memory, tool-use, classification learning, quantity discrimination, empathy, mirror self-recognition

Although the cognitive revolution was slow in coming to animal behaviour, in the last twenty years our understanding of animal cognition has advanced considerably. In particular, the highly social non-human primates have been the focus of intense interest, and research in comparative cognition has recently expanded to other large-brained and often social taxa, such as corvids (Bugnyar, 2002; Bugnyar & Heinrich, 2005; Clayton & Dickinson, 1998; Emery & Clayton, 2001, 2004), cetaceans (Connor, 1999; Herman, 1986; Reiss & Marino, 2001; Rendell & Whitehead, 2001), and social carnivores (Hare, Brown, Williamson, & Tomasello, 2003; Holekamp, 2006; Manser, Seyfarth, & Cheney, 2002; Miklosi, Topal, & Csanyi, 2004). Here we review what is known about the cognition of another large-brained and highly social group – elephants. Research conducted specifically into elephant cognitive abilities is still a fledgling enterprise, but we consider what we do and do not know, and compare the observable pattern with what we know about the best-studied mammalian group, the primates.

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Relative to their body size, the brain size of elephants is large, although not in the extreme range of humans or dolphins. The encephalization quotient varies between 1.3 and 2.3, depending on species (Cutler, 1979; Jerison, 1973), comparable indices to those of apes (Eisenberg, 1981). Encephalization gives a useful measure of investment in brain tissue relative to metabolic energy available in total, and thus indicates the cost to the animal of so large a brain (Byrne, 1996). It does not, however, give the best indication of 'brain-power': as with any computational system, to assess power it is the actual number of processing units available for use that is important (Byrne, 1996). Elephants have the largest absolute brain size among land animals: up to 5.5 kg in Asian elephants and up to 6.5 kg in African savannah elephants (Cozzi, Spagnoli, & Bruno, 2001; Shoshani, Kupsky, & Marchant, 2006). Although neurons are less densely packed in elephant brains than in primates', elephant brains nevertheless contain as many cortical neurons as do human brains (Roth & Dicke, 2005). Moreover, the pyramidal neurons are larger than in humans and most other species, with a large dendritic tree giving the potential for many more connections, and perhaps hinting at superior learning and memory skills (Cozzi, et al., 2001).

There is a considerable body of theory and supportive data to suggest that living in an extensive social network often correlates with, and likely promotes, cognitive sophistication (Byrne & Bates, 2007). To judge by the well-studied African elephant *Loxodonta africana*, elephant society may be one of the most elaborate discovered among mammals or birds. Elephant ranging is fission-fusion in nature: female matrilineal relatives and dependent offspring form family units that usually travel, forage and socialize together, but these family units can split up into smaller groups with irregular composition and can also join with members of other families to form larger groups (Moss, 1988). It is therefore possible that each individual elephant knows and differentiates among several hundred other individual elephants, far in excess of anything found in non-human primates. It has also often been suggested that superior primate intelligence derives from the technical sophistication that is allowed by prehensile hands, and the flexible motor control of the hands and fingers found especially in apes (Deacon, 1997; Napier, 1962). On this theory, also, a case may be made that the elephant might possess special abilities. The elephant's trunk is prehensile, and under exquisite brain control (Shoshani, et al., 2006), such that it can pick up and put down an egg without breaking it.

The large brains, societal complexity and advanced prehension of elephants have evidently evolved in parallel with those of primates. Elephants belong to the Afrotheria (Hedges, 2001; Murphy, et al., 2001), an ancient placental group that evolved between 105 and 40 Mya when the continent of Africa was isolated from other land masses. Among their closest relatives, elephants number golden moles, tenrecs, dugongs and elephant-shrews—Afrotheria is not a lineage in which large brains or social complexity are conspicuous. This means that if the cognitive abilities of elephants prove to resemble in any way those of humans, we can be sure that the resemblance results from convergent evolution rather than primitive retention. This, in turn, would enable more confident identification of the ecological contexts that promote these cognitive skills. Conversely, if elephant abilities prove wholly strange to those we are familiar with from the study of humans and other primates, understanding elephant cognition will broaden our knowledge of cognitive processes in general. It would seem that elephant cognition is an obvious topic for the highest priority.

Yet, to our knowledge, only 21 papers that describe specific attempts to assess elephant cognitive skills have to date been published in peer-reviewed scientific journals (see Appendix 1 for a list). Elephant vocal and chemical communication systems have been more extensively studied, but the cognitive implications of this work are usually not drawn out. Most of what is known about elephant behaviour comes either from structured observational studies of free-ranging African savannah populations, or from the anecdotes of people working with Asian elephants that are held in semi-captive conditions for use in the logging industry. Both observational studies and anecdotal reports have provided many examples of behaviors that appear to reflect advanced cognitive processing, but often without appropriate control observations. In this paper, we attempt to bring these different sources of information together to provide an evaluation of what can so far be judged of elephant cognitive skills, and what needs to be examined in the future. Given the current paucity of studies designed specifically to test elephant cognition, all conclusions that we draw must be treated as tentative and requiring further verification.

In order to organize this somewhat patchy information, we turn to current knowledge of what must be the best-studied order of mammals: the primates. The most comprehensive review of primate cognition remains that of Tomasello and Call (1997). Although the literature it evaluates is now a decade out of date, we borrow their organisation as a structure on which to hang our review of elephant cognition, allowing for straightforward comparison. (Note that this categorization may not truly reflect the organisation of the underlying cognitive apparatus.) Also like those authors, we take a cognitive approach in theorizing, throughout. In many of the cases we review, post hoc associative accounts could also be constructed; but we consider that formalism an unhelpful one for comparing animal abilities, particularly when flexible and sophisticated behaviour is deployed in real-world environments (see Byrne & Bates, 2006).

Elephant perceptual systems

Perception and cognition are intimately linked, and since elephants are so distantly related to primates (and indeed to any of the species traditionally studied in the psychologist's laboratory), we first provide a brief overview of what is so far known of their capacities.

Elephants are dichromats, with the same colour vision pigments as human colour-blind deutaneropes (Yokayama, Takenaka, Agnew, & Shoshani, 2005). With a greater concentration of rods than cones, their eyesight is thought to be good in dull light, but considerably reduced in bright light, reaching a maximum range of 46 m (Sikes, 1971). Certainly, their eyesight is good enough to detect the sometimes subtle postural displays that appear to be very important to elephants, such as ear-flapping, ear folding and trunk curling (Kahl & Armstrong, 2000). Elephants are also extremely tactile animals, frequently touching one another using their trunk, ears, tusks, feet, tail, and whole body. Tactile interactions between elephants can occur in aggressive, defensive, affiliative, sexual, playful and exploratory contexts. However, it is the olfactory and auditory senses that are generally considered to be the most significant to elephants, for obvious physical reasons.

Figure 1. At Amboseli, researchers can recognize over 1400 elephant individuals. Often the ears give the first clues to an individual's identity: overall shape, the pattern of veins and damage to the edges all differ. Photograph by the authors.

Elephants are capable of producing different sounds ranging from 5 Hz to over 9,000 Hz (Poole & Granli, 2003) resulting in a broad range of vocalizations from very low frequency rumbles to higher frequency trumpets and barks (Berg, 1983). However, elephants are specialists in the production of low frequency sound, with the most often produced vocalizations being low frequency rumbles; the lowest, infrasonic, components of these rumbles can be between one and two octaves below the lower limit of human hearing (Poole & Granli, 2003). Although the lower range limit of elephants' hearing has not been established, they are known to be more sensitive to low frequency sounds, and less so the high frequency sounds, than any other mammal so far tested (Heffner & Heffner, 1982).

Elephant groups are frequently highly dispersed; with groups often spread over 100m in diameter and, due to the fission-fusion social organisation, kin sub-groups can often be separated by several kilometers. Elephants use their low frequency rumbles such as contact calls to communicate over these long distances (Payne, Langbauer, & Thomas, 1986); these low frequency sounds are known to travel over 10km in optimal conditions (Garstang, Larom, Raspet, & Lindeque, 1995).

When an elephant rumbles, a replica of the airborne sound is also transmitted through the ground. Elephant sounds have been measured as travelling at 309 m per second through air and at 248-264 m/sec through the ground (O'Connell-Rodwell, Arnason, & Hart, 2000). Recent evidence suggests that elephants are able to detect these seismic vibrations, or Rayleigh waves, through two possible means: bone conduction and the use of massive ossicles of their middle ears (Reuter, Nummela, & Hemila, 1998), or possibly by mechanoreceptors such as Pacinian corpuscles in the toes or feet that are sensitive to vibrations (O'Connell, Hart, & Arnason, 1998).

Olfaction and chemical communication is also very important to elephants. Within the nasal cavity are seven turbinates (dogs only have five), scrolls of bones with sensitive tissues specialized for olfaction and hormone detection, containing millions of olfactory receptor cells (Shoshani, 1997). An elephant may be able to gain enough information by sniffing, but if not it will collect the substance on the tip of trunk and pass it to the Jacobson's or vomeronasal organ on the roof of the mouth for further analysis, behaviour known as the flehmen response.

Sources of odours used in chemical communication between elephants include urine, faeces, saliva and secretions from the temporal gland, a large multi-lobed sac with an orifice mid-way between the ear and eye (Langbauer, 2000; Rasmussen & Krishnamurthy, 2000). Elephants can frequently be seen to raise their trunks up in the air to smell, or use the tips of their trunks to explore the ground, for urine spots

and faecal matter, as well as the genitals, temporal glands, or mouths of other elephants (Rasmussen & Krishnamurthy, 2000).

Knowledge of physical environment

Space and objects

Extensive research has been carried out on how primates understand objects in their immediate environment, including object permanence and the ability to track hidden displacements; however, these topics have not been studied in elephants, so no useful comparison can be made. When it comes to the understanding of large-scale space, involving memory for and navigation within areas that cannot be apprehended from a single viewpoint, there are data for both species.

It has long been suspected that primates possess powerful and efficient 'cognitive mapping' skills (Mackinnon, 1978; Milton, 1981), but only in the last few years have strong tests been made (Janson & Byrne, 2007). Experimental studies have shown that capuchin monkeys are able to head directly for distant locations, and choose the most valuable to visit first (Janson, 2007); however, they do not compute routes that show efficiency over more than one target (i.e. solve 'the travelling salesman problem'). Observations of baboons have shown some ability in this direction, however: baboons take direct routes to distant, high quality resources that are likely to be exploited by other groups, returning later to consume other, more reliable resources by-passed earlier (Noser & Byrne, 2007b).

All primates whose travel has been mapped utilize a network of familiar routes, whether these are arboreal runways or terrestrial paths. The impression of limited spatial memory that this hints at may be misleading, however; when tamarins switched from their year-round fruit diet to feed on nectar, they travelled from tree to tree along quite different routes to their usual ones, routes that were highly direct (Garber, 1988). A similar navigational efficiency was earlier noted in orangutans; when a favoured fruit crop failed and individuals had to visit several trees, far apart in rainforest, their travel was a least-effort route (Mackinnon, 1978). These performances are often taken to imply Euclidian knowledge of space; but an alternative exists, a richly interconnected 'network-map' that allows efficient search from any location to any other (Byrne, 2000). Evidence that primate species do indeed rely on network-maps, rather than Euclidian knowledge equivalent to a 2D paper map, has come from both humans and baboons (Byrne, 1979; Noser & Byrne, 2007a). Primate route planning goes beyond spatial information: mangabeys have been shown to take into account the likely effect of warm, sunny weather on ripening fruit (Janmaat, Byrne, & Zuberbuhler, 2006). When passing close to a tree which held unripe fruit on their last visit, their decision whether to check the tree depends on the weather since their last visit: nor is this an effect of more enthusiastic ranging on warm sunny days, as the effect persisted when the conditions on the day of travel were statistically controlled.

Although the logistics of studying elephants in the field are entirely different to those in studying primates, there are nevertheless some data on which to make comparison with the primate picture.

African savannah elephants are known to move over very large distances in their search for food and water. Leggett (2006) used GPS collars to track the movements of elephants living in the Namib desert. He recorded one group living in the Namib desert travelling over 600 km in five months, and Viljoen (1989) showed that elephants in the same region visited water holes, some of which were over 60 km apart, approximately every four days. Even more impressively, elephants inhabiting the deserts of northern and southern Africa have been described travelling hundreds of kilometres to arrive at remote water sources shortly after the onset of a period of rainfall (Blake, Bouche, Rasmussen, Orlando, & Douglas-Hamilton, 2003; Viljoen, 1989), sometimes along routes that researchers believe have not been used for many years. These remarkable feats suggest exceptional cognitive mapping skills, reliant on the long-term memories of older individuals who travelled that path sometimes decades earlier. Indeed, a recent study has confirmed that family groups with older matriarchs are better able to survive periods of drought (Foley, Pettorelli, & Foley, 2008). Families with older matriarchs range over larger areas during droughts, apparently drawing on the knowledge of the older females about the locations of permanent, drought-resistant sources of food and water.

However, we cannot yet draw firm conclusions about the cognitive mapping skills of elephants, as data are restricted to field observations for which the strength of evidence is not entirely apparent. For example, we now know that elephants can detect low frequency rumbles at distances of several kilometeres (Garstang, et al., 1995; Langbauer, 2000), and can even detect seismic rumbles (O'Connell-Rodwell, et al., 2006), so it may be that elephants can follow the sounds of distant thunder to reach fresh water sources. Further investigation is required to determine how well this hypothesis accounts for the long-range movements of elephants. There are currently several study populations of African savannah elephants where the movements of multiple individuals are being accurately mapped with GPS tracking devices, so future insight into elephant cognitive mapping skills can be expected.

On a much smaller spatial scale, we recently showed that elephants are able to track the relative positions of their family members (Bates, et al., 2008b). We moved urine deposits from known individuals to positions where they would be

discovered by target individuals. With samples from individuals who were at least 1 km away, urine from kin produced significantly more interest from the target individual than samples from unrelated individuals. We also presented test elephants with urine deposits from related individuals actually present in their group that day, which were either walking some way ahead of the target elephant or behind it. We reasoned that if elephants are able to identify specific individuals from their urine, and each is continually updating its memory of where other key individuals are, then discovering a fresh urine deposit from an individual who was walking behind should violate its expectations. Target individuals investigated samples from family members behind them at the time of the test, significantly more than samples from individuals who were in front. From this, we concluded that elephants are able continually to track the locations of family members in relation to themselves, as either absent, present in front, or present behind (Bates, et al., 2008b). These results suggest that elephants are able to hold in mind and regularly update information about the locations of at least 17 other female party members, as well as implying that they recognize individual identity from scent and have some understanding of invisible displacement and person permanence. (We tested only scents of adult females, but it is presumably likely that individuals keep track of males and some immatures in addition.) That they can keep track of so many, independently moving companions implies that elephants have particularly large working memory capacity.

Tools and causality

With their opposable thumbs, primates are adept at object manipulation (Beck, 1980), with great apes having the greatest manual dexterity (Byrne, Corp, & Byrne, 2001; Napier, 1962). Tool use is widespread among animals, and is evident in all great apes and several monkey species (Beck, 1980). Tool use itself is not necessarily indicative of advanced cognitive processing, however. Instead, systematic tool manufacture or modification is recognised as cognitively more demanding, and is evident in only a handful of species: all four great apes in captivity (McGrew, 1989), though only chimpanzees and orangutans in the wild (Fox, Sitompul, & Van Schaik, 1999; McGrew, 1992); and the New Caledonian crow (Hunt, 1996, 2000b).

Both Asian and African savannah elephants have been seen to use multiple tool types for up to six different functions, mostly in the context of body care such as scratching and removing ticks, with one report of throwing mud during a competitive encounter with a rhino over access to a waterhole (Chevalier-Skolnikoff & Liska, 1993; Wickler & Seibt, 1997). Asian elephants presented with branches that were too long or bushy to make effective fly switches (fly-swats), a commonly used tool, modified them before use by either breaking off a side branch or snapping them in half (Hart, Hart, McCoy, & Sarath, 2001). Elephants may thus be added to the small number of animals that make tools. However, for an animal that frequently breaks branches while eating, the cognitive demands of extending this behaviour to manufacture fly switches are probably not great (Bates, Poole, & Byrne, 2008). Elephant tool modification does not compare in complexity to the manufacture of ant and termite dipping tools displayed by chimpanzees (Boesch & Boesch, 1990; Goodall, 1986), which even includes making two different types of tool for different stages of the same task (Sanz & Morgan, 2007); or with the serrated leaf probes and hook tools produced by New Caledonian crows (Hunt, 1996, 2000a).

Detecting causal reasoning in animals has, understandably, been a more elusive target. Several primate species have proved able to choose tools on the basis of relevant properties, even species like tamarins which do not naturally use tools (Hauser, 1997; Santos, Miller, & Hauser, 2003). Chimpanzees also gave evidence of some sort of causal understanding, when showing selectivity in what to copy (Horner & Whiten, 2005). When presented with opaque puzzle boxes, chimpanzees copied two actions made by a human demonstrator to release food. When the same boxes were transparent, revealing that one action was irrelevant, they missed it out and copied only the relevant action. The judgement of relevance, however, may have been based on a simple parameter. For instance, because the 'irrelevant' action made no physical contact with the food, the chimpanzees may only have attended to whether contact was made when they choose which actions to copy. Even chimpanzees have not performed impressively when confronted with a 'trap tube' task, in which poking the desired food item from the wrong side causes it to fall into a well and be lost (Limongelli, Boysen, & Visalberghi, 1995); the few individuals that solved the task did so only over several trials, raising concerns that they did not understand the issue. In contrast, rooks *Corvus frugileus*, another crow species that does not regularly use tools in the wild, solved the task rapidly and one individual showed immediate transfer to a different task that relied on the same basic insight (Seed, Tebbich, Emery, & Clayton, 2006).

Evidence of causal understanding in elephants is sparse. Nissani (2004) reports a string pulling experiment and a tube task conducted with two zoo-based female Asian elephants. The elephants were required to pull a retractable cord in order to obtain a food reward in the first experiment, and suck or blow through a tube to gain a reward in the second. Of the two subjects, one performed reasonably well, the other less so, and careful analysis of the pattern of results suggested that performance was dependent on trial and error learning, rather than an understanding of the causal relationships between the action and the outcome. Nissani also reported an

apparent lack of causal understanding by working Asian elephants, in dealing with a modified discrimination task (Nissani, 2006). The subjects were trained to remove food from a bucket only after they had touched the bucket lid, which during training was always placed on top of the bucket. In the test phase, the lid was placed next to the bucket instead of on top of it, so there was no need to touch it before accessing the food. Only in 3 of 77 trials did any elephants ignore the lid and reach straight into the bucket for the food. On the other trials, the elephants touched or even threw the lid away, as they had previously been trained to do. Nissani argued that this showed a lack of causal understanding by the elephants, but it might instead represent a lack of understanding of the task demands. Working elephants are trained from an early age to follow precise sequences of behaviour, and are punished for any deviation. Thus, in trials where the lid was placed next to the bucket, the subjects may have seen that the lid was now irrelevant, but nevertheless interpreted the task as one of following the trained practise. Until this experiment is repeated on animals that are normally allowed to exercise their behavioural choices freely, we should probably not draw conclusions about elephants' lack of causal understanding from it.

Indeed, some understanding of physical causality is suggested by the results of testing elephants on a well-known Piagetian task that depends on an understanding of the concept of support (Irie-Sugimoto, Kobayashi, Sato, & Hasegawa, 2008). Elephants were given a series of problems in each of which food bait was out of reach; but in some cases a bait item was supported by a tray which the elephant was able to pull. In all cases, one of the two elephants tested performed above chance in selecting the correct tray to pull, showing that it took a means-end approach to the problem and had some understanding of the notion of physical support.

Discrimination learning, features and categories

Tomasello and Call (1997) review extensive evidence that apes and monkeys are generally adept at learning feature discriminations and categories, both natural and artificial, In this, they do not differ from pigeons and rats, the animals more typically used in animal learning laboratories. Evidence suggests that elephants are similarly capable of discrimination learning, and moreover, that they have classification abilities that may exceed those of many animals.

One of the first systematic tests of elephants' discrimination learning ability was conducted by Rensch (1957) as he explored the long-term retention of a captive Asian elephant. Rensch taught a juvenile female Asian elephant 20 different visual discrimination pairs and six acoustic discrimination pairs; one pattern of each pair was rewarded. It took the female 330 trials to learn the first visual discrimination, but by the fourth and subsequent pairs it took her only ten trials to learn the correct target, showing that she developed a learning set as do Old World monkeys and apes (Passingham, 1981). The elephant was re-tested with the same visual discrimination pairs after a one-year delay, and she performed with 73-100% accuracy. As well as straightforward discrimination learning, there was some evidence that the elephant could transfer what she had learned about the features of the positive stimulus, and apply it correctly to novel stimuli. For example, she appeared to generalize over orientation. In the initial tests a + symbol was the correct choice; when subsequently presented with an x symbol for the first time, she immediately recognised it as correct. Generalization over size was also shown. The elephant was initially asked to discriminate between two stimuli showing black and white stripes, with the bands placed 2cm apart in the positive stimulus and 4cm apart in the negative stimulus. At a later date she was presented with novel striped stimuli, this time with the spacing either 1.5cm or 2cm. She chose the correct stimulus of the thinnest stripes – 1.5cm, even though in previous trials the 2cm stripes had been the correct choice. However, with only two such examples in this paper, it is difficult to draw firm conclusions. In contrast to Rensch's paper, a discrimination task conducted on working Asian elephants (Nissani, Hoefler-Nissani, Tin Lay, & Wan Htun, 2005) reported that some of the 20 animals tested never learnt to pass the tests although others did perform comparably to the young female tested by Rensch. There was an age effect in these results, however, with more individuals over the age of 20-30 years unable to acquire the discriminations.

We conducted a field experiment in the Amboseli National Park, Kenya, that may be seen as a more ecologically valid test of elephant feature learning and categorization, presenting individually known elephants with garments that gave either visual or olfactory information about their human wearers (Bates, et al., 2007). We used garments that had been worn by members of two different ethnic groups that pose different levels of danger to elephants. In the first set of trials, we separately presented elephant groups with three different red cloths, using a within-subjects design. Each of the cloths had been worn either by a Masaai warrior, or a similar aged man from the agricultural Kamba tribe, or by no one at all. The only thing that differed between the cloths was therefore the smell, derived from the ethnicity or lifestyle of the wearers. With access only to this olfactory information, the elephants showed significantly greater flight reactions to garments worn by Masaai warriors than similar age Kamba men. In a second experiment, elephants in the same population were presented with two cloths that had not been worn by anyone, but here one was white - a neutral stimulus, and the other was red - the colour that is ritually worn by Masaai warriors. With access only to these visual cues, the elephants showed significantly greater reactions to garments worn by Masaai warriors than similar age Kamba men, often includ-

ing signs of aggression. We concluded that elephants are able to categorize a single species (humans) into subclasses, an ability that relies on sophisticated discrimination learning and classification (Bates, et al., 2007).

The numerous vocal, gestural, and chemical signals used by elephants also suggest considerable classification abilities in elephants. Over a hundred different gestural displays have been described for African elephants (Kahl & Armstrong, 2000; Poole & Granli, 2003); tens of different vocalisations have been recorded (Langbauer, 2000; Poole, Payne, Langbauer Jr, & Moss, 1988); and chemical signals are known to accurately indicate sexual states in both males and females (Rasmussen & Schulte, 1998). Although recognition of most of the visual and vocal displays has not been formally tested, the fact that so many distinct signals exist is suggestive of subtle discrimination learning and elaborate categorisation. Where playback experiments have been used to test reactions, this notion has been supported (McComb, Moss, Sayialel, & Baker, 2000; Poole, 1999). From their reactions, it was clear that elephant calls convey information about musth state, and some information about the caller, at least familiarity and perhaps individual identity. Thus, although primates have been tested much more extensively in this area, there is reason to think that knowledge of features and categories that can be learnt by elephants, and their ability to categorize and classify entities in the world, may at least match those of any primate.

Quantities

Rensch (1957) presented his five year-old female Asian elephant with number discriminations: she was able to distinguish 3 from 4 dots regardless of their arrangement and spread. Irie-Sugimoto et al (2008) tested the relative quantity judgements of Asian elephants. They presented five captive Asian elephants with two baskets containing different quantities of food, and the elephant had to choose the basket with the larger amount. All five elephants chose the larger quantity significantly more often than the smaller, performing with 67-89% accuracy. Elephants were as good at picking the larger quantity when it was only slightly bigger (e.g. 6:5) than when it was considerably bigger (e.g. 5:1), and performance did not vary with the total number of items presented, up to 12. In a second experiment, four additional Asian elephants watched and listened to the baskets being baited, but they could not see the final amounts in the baskets. All elephants chose the basket containing the larger amount, significantly more often than expected by chance, performing at 72-82% accuracy. As in the first experiment, the elephants did not exhibit disparity or magnitude effects, in which performance declines with a smaller difference between quantities, or the total quantity increases, respectively, in striking contrast to the performance of great apes and even human

infants in similar relative quantity judgement tests (see Anderson, Stoinski, Bloomsmith, & Maple, 2007; Beran, 2001; Boysen, Bernston, & Mukobi, 2001; Feigenson, Carey, & Hauser, 2002; Xu & Spelke, 2000). It is not yet known what cognitive mechanisms underlie the Asian elephants' numerical ability, but it may be that elephants are able to keep track of a larger number of items in immediate, working memory than can great apes including humans, and that when relative quantity judgements of larger numbers of items are explored then disparity and magnitude effects will emerge. If so, then there is a clear parallel with the ability of African savannah elephants to keep track of the movements and positions of a remarkable number of family members. Indeed, the unusual numerical abilities of elephants may derive, in evolutionary terms, from the elephant's need to monitor and coordinate movement of their extensive families.

The social environment

Knowing about others and their interactions

Whilst individual recognition is considered an important component of animal social life, experimental demonstrations of the ability are relatively sparse. Monkey and ape species, however, are known to understand both the direct and third party relationships of others (Cheney & Seyfarth, 1990), and alliances and coalitions with specific individuals are a prominent feature of monkey and ape sociality (Harcourt & deWaal, 1992). Note that knowledge of third party relationships is not restricted to large brained species. Some fish and bird species have also been found able to track the relative relationships of third parties, through what has been termed 'eavesdropping' on the behaviour of others (e.g. Oliveira, McGregor, & Latruffe, 1998; Otter, et al., 1999).

Our urine-moving experiments, discussed above, showed that elephants have knowledge of individual identities, and are able to recognise and keep track of at least 17 different female family members (Bates, et al., 2008b). McComb et al (2000), using experimental play back of long-distance contact calls in the same Amboseli population, showed that each adult female elephant was familiar with the contact-call vocalisations of individuals in an average of 14 families in the population, totalling around 100 elephants. When the calls were from a familiar family, i.e. one that had previously been shown to have a high association index with the test group, the test elephants contact-called in response and approached the location of the loudspeaker. When a test group heard unfamiliar contact calls (from groups with a low association index with the test group), their spatial cohesion increased, and they retreated from the area. Whether this vocal familiarity is based on individual recognition is uncertain, however. It currently remains untested whether elephants understand and take advantage of third-party relationships.

Field observations of African elephants show clear coalitions and alliances (Bates, et al., 2008a; Moss & Poole, 1983), but reciprocity is less clear – there may be an element of this in the formation of coalitions, but it has not been demonstrated formally. Asian logging elephants frequently work together to roll heavy logs up ramps, which is certainly cooperative, but they have been trained to work like this so may not themselves understand the cooperation (Rensch, 1957).

Cooperative problem solving is observed fairly regularly in long-term behavioural studies of African elephants (Moss, 1988). For example, two or more individuals may work together to help individuals that are trapped by muddy river banks or drainage ditches (Bates, et al., 2008a), or to chase off vehicles when an individual is darted for veterinary purposes (Moss, personal observation). In the Amboseli population, related individuals have also been observed to form coalitions when attempting to retrieve infants that have been commandeered by other, unrelated families (Moss, personal observation), and this could also be viewed as cooperative problem solving.

Social strategies and communication

African savannah elephants are known to have an extensive gestural and vocal repertoire (Poole & Granli, 2003). Moreover, as previously noted, they discriminate the contact calls of familiar and strange individuals (McComb, et al., 2000). Social knowledge apparently accrues with age: old females have the best knowledge of the contact calls of other family groups (McComb, Moss, Durant, Baker, & Sayialel, 2001). Monkey and ape vocalizations sometimes encode 'functionally referential' information, that is, hearers react to the calls in the same way as they would to entities in the world, such as specific predators (Seyfarth, Cheney, & Marler, 1980; Zuberbuhler, 2000). Whether anything similar is latent in elephant vocalizations, however, is unknown.

Deception and manipulation have been hot topics in primate work since the 1980s (Byrne & Whiten, 1988; de Waal, 1982). Deceptive tactics have been reported in all taxa of primates, with frequency of use well predicted by the species' neocortex size (Byrne & Corp, 2004), and in great ape species at least some deception appears to be done intentionally, with some understanding of others' mental states (Byrne & Whiten, 1992). In elephants, there is only one report of possible deception (Morris, 1986): certain captive elephants in a zoo were noted to finish their ration of hay quickly, and then move near others still eating, swinging their trunks in an 'aimless' manner, but occasionally eating some of their hay. It is not clear, however, whether the trunk-swinging was used tactically, and whether the other elephants were deceived. Researchers on wild populations report no deception at all, so it may be that the extensive social network of elephants renders deception an inappropriate way for them to manipulate others.

Social learning

Although as yet there are no formal studies of social learning in elephants, or observations of behavioural traditions, it would be unwise to conclude that such a long-lived, slowly maturing, highly social species does not learn through observing group members. The impressive spatial knowledge shown in some populations, for instance, is surely acquired by young individuals from following older, more knowledgeable relatives.

Elephants may eventually be shown to possess social learning abilities absent in non-human primates. For instance, there is some evidence of vocal imitation in African elephants (Poole, Tyack, Stoeger-Horwath, & Watwood, 2005), and even one intriguing report of a captive Asian elephant copying human speech, although this has not yet been formally verified. Non-human primates lack any significant abilities in vocal imitation (Janik & Slater, 1997). Also, currently unpublished data suggests that older female African elephants may teach young, naïve, nulliparous females how to behave when they come into oestrous for the first time (Bates et al, in preparation). Despite some suggestive observations (Boesch, 1991), there is no consensus that any species of non-human primate is able to teach (Caro & Hauser, 1992; Thornton & Raihani, 2008)

Thus, while there is little evidence on which to compare the social learning skills of elephants directly with those of the extensively studied primates, this is representative of a lack of research effort on the topic rather than a lack of social learning ability in elephants. Reports of vocal imitation and potential teaching behaviour suggest this is one area where greater research effort could prove particularly fruitful and instructive.

Theory of Mind

Studies of primate cognition that are embraced by the portmanteau term 'theory of mind' include those on understanding the gaze and perception of others, understanding intentions and attention, understanding knowledge and beliefs, and understanding the self. There has been much speculation as to the cognitive underpinnings of theory of mind and self-recognition abilities, but as yet there is no consensus (Byrne & Bates, 2006; Gallup, 1985; Povinelli & Vonk, 2003; Tomasello, Call, & Hare, 2003).

There is experimental evidence that many species of primate follow gaze, even where the gaze is directed behind obstructions (Tomasello, Hare, & Agnetta, 1999). Puzzlingly, individuals of the same species often fail to give evidence that they can use gaze as a cue to object choice, but recent

to understand the operation of mirrors: continuing to make social responses, as if to another individual of their species, or habituating to mirrors altogether and paying no further attention to them. Monkeys, however, do learn to understand the geometric properties of mirrors, using them to detect the presence of individuals that appear behind them, or to reach food rewards more successfully by locating their reflection in a mirror (Anderson, 1984). However, they signally fail to recognize a reflection of their own face as such, despite extensive experience. In contrast, members of all species of great apes can learn to interpret a mirror reflection or CCTV image of their face as 'themselves', although not all individuals ever do so (Gallup, Jnr, 1970, 1982; Patterson & Cohn, 1994).

Recent analysis of behavioural records of the African savannah elephants of Amboseli NP suggests that they understand the emotions and the intended goals of others, acting empathically towards individuals who are distressed and helping them in ways that were appropriate to their predicament (Bates, et al., 2008a). A description of the reactions to a dying and subsequently dead matriarch by both family members and unrelated elephants further suggests that elephants can act empathically (Douglas-Hamilton et al, 2006). However, Bates et al (2008a) did not find any positive evidence for the capacity to understand others' attention, knowledge or beliefs. The same could be said of field studies of apes, so explicit tests of elephants' understanding of others' mental states may be worthwhile.

Nissani (2004) modified experiments devised by Povinelli and Eddy (1996) to examine what two zoo-based Asian elephants understood about visual attention. Povinelli and Eddy had found that chimpanzees chose to beg from a person whose whole body was oriented toward them rather than oriented away, and these two elephants performed similarly. However, chimpanzees did not discriminate between people according to their head orientation alone: for instance, when offered a choice between two people standing sideways-on, one with the head turned 90 degrees to look at the chimpanzee subject, and one not, or between two people both whole body oriented toward them but one with the face covered or with a bucket over their head, the chimpanzees performed at chance. Nissani gave 8 trials of each sort to each of the two elephants, and none of the results were individually significant. However, with sideways body presentation it appeared that the elephants were able to take account of the person's face orientation (6/8 and 7/8 trials successful, respectively). It may indeed be that straight copies of studies used with monkeys and apes are systematically unsuitable for probing elephant cognition; new and creative experimental designs may be required. Monkeys and apes predominantly use vision to learn about the social world. For elephants, audition and olfaction are demonstrably more important than vision, with comparatively much larger brain areas dedicated to these

Figure 2. Collecting earth soaked with recently-deposited urine, for use in conducting "expectancy violation" experiments at Amboseli. The presence of an individual is artificially simulated by moving urine deposits. Photograph by the authors.

work suggests a resolution. Lemurs were found to use gaze successfully as a cue, by following gaze and then choosing objects in the direction they were looking, a tendency that the researchers called 'gaze priming' (Ruiz, Gómez, Roeder, & Byrne, 2009). However, neither gaze following nor gaze priming were done rigidly and success rates were relatively low, perhaps explaining apparent failures in earlier work that did not test gaze following and cueing in the same task. In addition, field observations suggest that monkeys and apes are able to understand the geometric perspective of others (Byrne & Whiten, 1992); this has been confirmed experimentally only in the case of the chimpanzee (Hare, Call, Agnetta, & Tomasello, 2000). The observational data, based on collated records of deception, also implied that only apes are able to take account of the knowledge of competitors (Byrne & Whiten, 1992). Again, this was finally confirmed experimentally in the case of the chimpanzee (Hare, Call, & Tomasello, 2001; Tomasello, et al., 2003) and the orangutan (Cartmill & Byrne, 2007), after several years of explicit denials of the possibility (Povinelli, 1993; Povinelli & Eddy, 1996; Tomasello & Call, 1997).

An intriguingly similar distribution of ability across primate phylogeny has also been uncovered by study of animal reactions to mirrors. Most animals plainly cannot learn

areas than visual cortex (Hakeem, et al., 2005; Shoshani, et al., 2006). It therefore seems probable that tests using auditory or olfactory stimuli will be more relevant to elephants, and more likely to accurately measure their mental abilities.

One area in which it will not be possible to avoid the visual domain is that of mirror self-recognition; accounts of two tests in Asian elephants have been published, with somewhat contradictory results. Both relied on Gallup's (1970) 'mark test' paradigm. In this, the subject is first given extensive experience with a mirror. If signs of self-recognition are observed, such as self-monitoring while making repetitive or unusual movements, then the mark test is applied. Surreptitiously, for instance while the subject is anaesthetized, a conspicuous mark is applied to its body in two places, one visible directly and one not. The subject is then observed for a period without access to a mirror, to control for the possibility that the marks can be detected by scent or tactile sensation. Provided the subject examines only the visible mark, and not the concealed one, the mirror is then restored. Then, once the subject catches sight of its image in the mirror, the critical observation – seen in many great apes – is that it suddenly touches and explores the concealed mark, while monitoring the mirror to guide its hands. Povinelli (1989) followed this procedure when testing two elephants: however, he observed no signs of self-recognition and both individuals subsequently failed the mark test (see also Nissani & Hoefler-Nissani, 2007). He concluded that Asian elephants do not show self-recognition. However, these elephants were only given a few days exposure to the mirror prior to testing; chimpanzees that have passed the mark test have typically had weeks or months of prior mirror exposure. In the second experiment, because their three elephants could not be separated, Plotnik et al (2006) used sham marking to control for the possibility that the subjects might be able to detect a mark by non-visual means. They report that one of three adult females they tested did show mirror self-recognition: she touched the visible mark several times, but never the sham mark. Moreover, all three elephants showed suggestive behaviour in front of the mirror, prior to any marking, most strikingly cases where "the elephant is standing AT the mirror, and moves its head in and out of mirror view, like a kid playing with his mirror image by running in and out of view of it" (Josh Plotnik, personal comm.). However, with only one subject giving a positive response to the mark test, it is crucial that this response should be a convincing one. The initial response shown by the 'successful' elephant, after spending time in front of the mirror, was to walk away for 7 minutes. Then she returned and moved in and out of mirror-view a couple of times, then moved away again, still having shown no mark-touching. Finally, she moved away from the mirror and only then, when away from the mirror did she first touch the mark with her trunk. This pattern is so different to that observed in the great apes that recognize themselves in mirrors that it cannot be considered definitive; but we suspect that future data will show that elephants do indeed have the competence to recognize themselves in a mirror.

Summary

A recurring theme throughout this survey has been the stringent limitations on the extent to which elephant and primate cognition can be satisfactorily compared. It is not just that less is known, for both practical and historical reasons, about elephant cognition, although that is certainly true. But in addition the positive things that we do know about cognition within the two families are often hard to compare. Repeatedly, the ready availability, ease of manipulation and straightforward motivation of captive primates has enabled experiments to be done which are not easily done with elephants, and have yet to be attempted. At other times, experiments with elephants have revealed abilities that are not proven with primates; for instance, our studies with olfactory social stimuli enabled demonstration of individual identity recognition in elephants, an ability not so far shown experimentally in primates. Yet the differences we have reviewed are often more likely, perhaps, to reflect differences in study methods and facilities available than to point to any profound difference in cognition.

Undoubtedly, elephants perform well on laboratory tests of learning, discrimination and memory, and spontaneously engage in simple forms of tool use – no obvious differences from primates are apparent here. Similarly, it seems likely that elephants, like the great apes, have the cognitive capacity to recognize themselves in a mirror. When it comes to categorization, some intriguing findings have recently emerged that may point to capacities unusual for mammals. In number discrimination, elephants like primates are able to distinguish quite small quantity differences – yet strangely they showed no effect of the size difference in making their judgements, nor any variation in performance with the total number of items presented. One possibility is that this lack of disparity and magnitude effects is a result of unusually large working memory capacity: for elephants, even groups of 5-6 items can be appreciated and compared in the manner that humans and other great apes can appreciate groups of 2-3. Wild elephants have been shown to sub-categorize humans into groups according to the varying levels of risk to them that different groups present, and to make this categorization on the basis of scent or colour, independently. In the social realm, there is no doubt that elephants show empathy into the problems faced by others as well as reacting to their expressed emotions, but much more work needs to be done before the initial hints of elephant abilities in cooperation, imitation and teaching can be properly understood. In contrast to the lack of any special signs of cogni-

tive ability in laboratory tests of memory, data from the field suggest that the elephant's vaunted reputation for memory may have a basis in fact, in two ways. Faced by the need to remember spatial information over very long periods, for instance the locations of waterholes in a desert, it is thought that elephants are able to re-find, over vast distances, places not visited for many years: elephants may be specialized for cognitive mapping. And in the immediate social realm, the ability to keep track of the current locations of 17 or more family members also seems remarkable. As with the data on quantity judgements, one possibility is that elephant working memory is larger than in humans or other great apes.

We finish with two speculations. First, we doubt that it is a coincidence that the tests giving the strongest positive results so far are those based on abilities elephants show naturally in the wild, whereas tests that do not perhaps lend themselves to the natural environments of elephants have often been inconclusive. Thus, in order to go beyond the somewhat sparse picture we have painted here, and explore elephant cognitive skills in causal reasoning, social learning, and theory of mind, we suspect that investigation using ecologically valid stimuli will be required. Second, if elephant and primate cognition do indeed prove to be similar in many ways, as still seems entirely possible, a convincing explanation will be needed. Elephants are more closely related to aardvarks, hyraxes and dugongs than they are to primates (Murphy, et al., 2001): by contrast, rats and people are close cousins. Any coincidence in cognitive skills between elephants and primates, therefore, points to convergent evolution for specific abilities, so the future study of elephant cognition offers the potential to understand better the evolutionary forces that select for particular mental skills.

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Appendix

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